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A comment on the validity of the British Great Tit *Parus major newtoni*

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The Great Tit in Britain is today recognized as a distinct subspecies *Parus major newtoni* solely on the form of its bill (Cramp & Perrins 1993). This was not always so. The type description (Appendix) given by Prazak (1894) in connection with **Typus**: K.u.k. natul. Hofmuseum in Wien. Nr. 10664, male, which was based on 19 British specimens examined at the Hofmuseum in Vienna, lists a suite of diagnostic plumage characters, none of which has withstood closer scrutiny (Hartert 1907, Witherby 1920, Saunders 1927, Witherby *et al.* 1938–41), and states that it is smaller than *P. m. major*, but makes no mention of the bill. We are told neither the sex ratio of the British series (although they were probably males) nor the origin of the *P. m. major* specimens with which they were compared. The description gives a hint that they are from central Europe, perhaps Austria. They are

therefore probably not from neighbouring populations, but widely separated along what is now recognized to be a cline of body-size (in which British Great Tits are amongst the largest forms, not smaller as stated in the type description) and colouration (Snow 1953), and lying on different sides of the Alpine barrier (Harrison 1945).

The first clear mention of a racial difference in the bill comes from Hartert (1907) who reported:

(*P. m. newtoni* is . . .) "*Easily distinguished from* Parus major major *(typical in Scandinavia, Germany, France, Holland, Belgium etc.) by its stout, powerful bill. The alleged differences in colour are not constant.*" E. Hartert (1907)

Between 1907 and 1945, no systematic analysis of bill differences was made. Hartert (1907) himself gave no quantitative evidence for his assertion. Witherby (1920) illustrated the difference in bill form, and stated that in *newtoni* the bill tended to be longer, stouter, and with a decidedly straighter culmen than that of *major* although the differences were ". . . *more apparent by comparison than by measurement*". No other reliable differences had been found. In updating Saunders (1927) *Manual of British Birds*, Eagle Clarke repeated that *newtoni* differed only in the form of the bill, but again gave no quantitative evidence. Although Witherby *et al.* (1938–41) presented some ranges of bill measurements for *newtoni* and *major*, their data are inadequate to determine statistical significance.

So by 1945 all standard works agreed that the British Great Tit was distinct on bill characters alone although none gave any substantial evidence in support of this. In overall size and colour, they agreed that there was no consistent difference from nominate *major*. Harrison (1945) realized that the existing taxonomy was essentially unsupported. In scanning through several series of *newtoni* and *major* skins, he noticed that the reported bill differences were not at all clear cut. Hence in 1945 he attempted, by examination of 50 *newtoni* and 50 *major* skins at the British Museum (Natural History), to quantify this difference to assess its extent and consistency. He found that 42% of *newtoni* skins had a straight culmen (judged by eye) while only 4% of *major* had (96% had a decurved or convex culmen). He also found a tendency for *newtoni* to have a greater bill coefficient (depth × breadth) than *major*. I have tested Harrison's data by *t*-test and find this 'tendency' to be highly significant statistically.[1] Harrison's (1945a) data were taken to support the accepted status of *P. m. newtoni* as a distinct subspecies although Harrison accepted that the southern English populations were not genetically isolated from the continent so that the situation might be rather 'fluid' between the nearest populations of the two races.

Harrison (1945a) clearly went to great lengths to standardize his data collection as far as was possible. He used only adult males. Care was taken that all *major* specimens came from north and west of the Alps, which he recognized as a possible barrier to gene flow (Harrison 1945a).

[1]A test of Harrison's data (t_{98}=10.73, P<0.001).

Hence we must assume that specimen selection and the measurement itself were carried out systematically. There are, nevertheless, two problems remaining. The first concerns use of the 'bill coefficient' itself. Many, perhaps most, Great Tit skins in the Natural History Museum show considerable mandibular retraction. In most, this has affected only the lower mandible, but in some the upper mandible is depressed also. This displacement is caused by contraction of the jaw muscles on drying. Hence in many cases, the bill is set open, and even when closed, the lower mandible may be retracted into an unnatural position. Bill depth cannot be measured reliably in these specimens. These problems should have less effect on the measurement of the bill length. The second problem (and one which was unknown to Harrison) arises from my own recent studies on the Wytham Great Tit population near Oxford showing considerable seasonal change in bill size and shape (Gosler 1987a, 1987b, 1990). In those papers I showed how the bill-index (bill depth/bill length), an ecologically-relevant character, changed within individuals in relation (probably in response) to changes in diet from hard seeds, such as beechmast, in winter to soft invertebrates, especially caterpillars, in the spring. The bill was therefore stoutest in winter, the first and fourth quarters of the year, and most slender when the birds bred in the second and third quarters of the year.

In this paper I compare bill size and shape of *newtoni* and *major* skins from the British Natural History Museum, Tring, and test whether differences between them might have arisen from a seasonal bias in collection of the two series. The validity of such characters for infraspecific taxonomy is briefly considered.

Methods

Two analyses were carried out. The first was a simple simulation study which aimed to determine whether apparent geographical variation could be generated from seasonal changes in the bill through biases among populations in the dates of collection. The second directly compared bill-length and culmen-curvature in *newtoni* and *major* skins in the Natural History Museum.

For the simulation study, I recorded the dates of collection of all *P. major* (301 in all) skins from the countries listed in Table 1. This table also shows the numbers of skins available from each quarter of the year (first quarter=Jan–March etc.). A simulation data set was then constructed in which the year-quarter was replaced by the observed mean bill-index for the appropriate year-quarter of Great Tits trapped in Wytham during routine trapping (see Gosler 1987) between 1982 and 1997. These values are given in Table 2. The bill-index was calculated as the bill-depth at the deepest point of the gonys divided by the bill-length to skull (as Gosler 1987). Bill measurements were taken to 0.05 mm with a vernier caliper. Mean bill-indices were calculated for each country from these substituted values and the whole data set, tested by one-way ANOVA for differences among country means.

For the direct comparison I selected skins of 40 British and 40 continental adult males. The former were the first 40 skins encountered

TABLE 1

Sample sizes available at the Natural History Museum from each country by sex and year-quarter (Q1, Jan–Mar, Q2, Apr–Jun, etc)

	Males Year-quarter				Females Year-quarter			
Country	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4
Norway	0	0	1	2	0	0	1	2
Sweden	6	0	4	6	2	0	0	1
France	13	0	4	19	4	1	4	12
Holland	1	2	0	1	1	2	0	0
Denmark	2	0	0	3	0	0	0	0
Germany	2	0	0	5	1	0	0	1
Belgium	0	0	1	0	0	0	0	2
England & Wales	26	12	6	47	18	4	2	27
Scotland	10	7	3	5	5	2	2	4
Ireland	3	0	0	3	6	0	0	3

TABLE 2

Mean bill indices (bill-depth/bill-length) observed in live, trapped Great Tits at Wytham Woods, Oxford. Means are given for each year-quarter calculated from measurements of 4949 individual Great Tits (2387 male, 2562 female) trapped between 1982–1997.

Year-quarter	Mean male bill-index	Mean female bill-index
1 (Jan–Mar)	0.34619	0.33549
2 (Apr–Jun)	0.34276	0.32645
3 (Jul–Sep)	0.34507	0.33250
4 (Oct–Dec)	0.34907	0.33559

from England (because Clancey 1945 and Harrison 1945b considered that some Scottish populations seemed closer to *major* in the form of the bill). The continental birds comprised all measurable skins from France (30), Holland (4), Denmark (5) and Belgium (1). From each I recorded the month of collection and measured the bill-length as above. To measure curvature of the culmen each skin was photographed in lateral view. The photographic negatives were later examined under a low-power microscope fitted with an eye-piece graticule. The straight edge of an acetate film strip was laid along the image of the culmen from the bill's base and the distance (t) from the bill tip to the point at which the acetate edge parted from the culmen (point of curvature) was measured with the graticule. The index of curvature was then calculated as this distance expressed as a percentage of the total bill-length (t/bl in Fig. 1). Hence if the whole culmen was straight, the index would be 0/bill-length=0%, and if just the first (proximal) quarter was straight an index of 75% would be found etc. To test the repeatability of this measurement, a subset of 17 negatives, selected at random, was remeasured by an independent observer. These

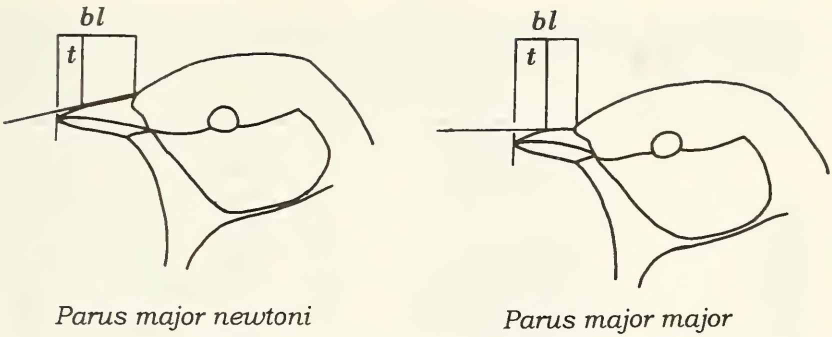

Figure 1. The measurement of culmen curvature from photographic negatives. The index of curvature is taken as *t/bl* (see text). Two examples are given, which also illustrate the bill differences between *Parus major newtoni* (here with a curvature index of 25%) and *P. m. major* (here 50%). The examples, which are similar to drawings in Witherby (1920), p. 227, were drawn from photographs.

measurements were significantly correlated with my own,[2] indicating that, while not perfect, the curvature index should be sufficiently reliable to compare populations.

Bill-length and curvature were each analysed by means of a two-way ANOVA with season and population (British or continental) as factors together with their interaction. Unfortunately, no adequate British skins were available from the third quarter of any year. To overcome this problem, which would have made impossible the fitting of an interaction term, I calculated the year-quarters as Q1. Dec–Feb, Q2. Mar–May, Q3. Jun–Aug and Q4. Sep–Nov. This small adjustment provided adequate sample sizes while retaining the broad pattern of seasonal change in the bill.

Results

Table 3 shows the mean bill indices calculated from the simulated data set constructed from Wytham data. The differences across countries were statistically significant for both sexes[3] indicating that apparent geographical variation could be generated simply from date-biased sampling from a seasonally-varying population. Of course, this does not necessarily mean that it had been.

Table 4 shows mean bill-lengths and percentage curvatures by seasons for the 40 British and 40 continental skins measured and photographed. The two-way ANOVA of bill-length found both a

[2]Measurements of culmen curvature made by an independent observer were significantly correlated with my own (r_{15}=0.685, P<0.01).

[3]Differences across countries were statistically significant for both sexes (males: $F_{9,184}$=2.44, P=0.012, females: $F_{9,98}$=2.09, P=0.044).

TABLE 3

Mean bill indices calculated for each sex and country from a simulated dataset derived by substituting the mean indices from Wytham (Table 2) for the season (year-quarter) when collected, shown in Table 1. Differences among these means were statistically significant (see text).

	Mean ± 1 s.d. male Bill Index	*n*	Mean ± 1 sd. female Bill Index	*n*
Norway	0.34774 ± 0.00231	3	0.33456 ± 0.00178	3
Sweden	0.34699 ± 0.00172	16	0.33552 ± 0.00006	3
France	0.34759 ± 0.00163	36	0.33455 ± 0.00222	21
Holland	0.34519 ± 0.00305	4	0.32946 ± 0.00522	3
Denmark	0.34792 ± 0.00158	5		0
Germany	0.34825 ± 0.00141	7	0.33554 ± 0.00007	2
Belgium	0.34507 ± 0	1	0.33559 ± 0	2
England & Wales	0.34715 ± 0.00225	91	0.33472 ± 0.00251	51
Scotland	0.34567 ± 0.00224	25	0.33367 ± 0.00339	13
Ireland	0.34763 ± 0.00158	6	0.33552 ± 0.00005	9

highly significant population effect,[4] with the British skins being longer-billed, and a significant seasonal effect,[5] but no significant interaction between population and season, indicating that the seasonal pattern was similar in both populations. The two-way ANOVA of culmen-curvature again revealed a highly significant population effect,[6] but no significant seasonal effect or season × population interaction. So culmen shape may be more constant than bill-length. Finally it is worth mentioning that bill-length and curvature were uncorrelated, either across all 80 skins[7] or within their respective populations.

Discussion

The present analyses have shown quantitatively that seasonal variation observed in bill-shape within individuals is sufficient to generate the appearance of significant geographical variation if collection dates are biased. However, in reality, the differences in bill-length and curvature between populations were much greater than could be accounted for by such bias alone. Furthermore, these two bill characters, which Witherby (1920) considered taxonomically relevant but essentially unmeasurable, prove not to be so intractable, and are confirmed to differ in a highly significant way between populations. It is also of interest to note that the seasonal pattern described from the Wytham population was also repeated in the skins of both British and continental origin.

[4]Two-way ANOVA population effect on bill length ($F_{1,72}$=9.69, P=0.003).

[5]Two-way ANOVA seasonal effect on bill length ($F_{3,72}$=3.96, P=0.011).

[6]Two-way ANOVA population effect on culmen curvature ($F_{1,72}$=9.69, P=0.003).

[7]Bill-length and culmen curvature were uncorrelated (r_{78}= − 0.08 n.s.).

TABLE 4

Mean (± 1 s.d. and *n*) bill-lengths and percentage culmen curvature, by year-quarters (Q1, Dec–Feb, Q2, Mar–May, etc.) of 40 British and 40 continental male Great Tits from the Natural History Museum. Bill-lengths differed significantly between seasons and populations, bill-curvature differed between populations (see text)

		Year Quarter			
Measure	Country	Q1	Q2	Q3	Q4
Bill-length	British	12.99 ± 0.524 (13)	12.38 ± 0.409 (12)	13.70 ± 0.0 (1)	12.97 ± 0.478 (14)
(mm)	Continental	12.53 ± 5.85 (9)	12.27 ± 0.32 (7)	12.40 ± 0.0 (1)	12.49 ± 0.464 (23)
Bill-curve	British	36.6 ± 9.25 (13)	39.8 ± 11.46 (12)	21.9 ± 0.0 (1)	36.8 ± 8.77 (14)
(%)	Continental	45.6 ± 10.47 (9)	45.5 ± 11.53 (7)	50.0 ± 0.0 (1)	44.7 ± 10.91 (23)

This study therefore confirms the views of earlier workers that the bills of British Great Tits differ on average from those of their nearest continental conspecifics. However, a question remains as to whether this justifies recognition of *P. m. newtoni* as a distinct subspecies. Amadon & Short (1992) define a subspecies as '. . . a recognized allopatric subpopulation which is (still) genetically compatible with other subpopulations, but is set apart by a concordant array of genetic and phenotypic characters'. From their evolutionary approach to infraspecific taxonomy, they view subspecies as potential, if not incipient, species. The phenotypic plasticity of the Great Tit bill, that I have already demonstrated, in which the form of the bill tracks changes in the bird's diet, must call into question the validity of a taxon based solely upon it. Furthermore, the greater length of the bill in British Great Tits is consistent with their greater body-size, and this is itself consistent with its position on a cline (Snow 1953). One is left then with the fact that the bill is somewhat deeper than expected from body-size (Snow 1953), but with little idea of the source of this variation, and with an uneasy sense that this alone hardly constitutes a 'concordant array of . . . characters'. At least as far as currently described characters are concerned, the British Great Tit may be more appropriately considered as a deme '. . . a localized diagnosable subpopulation of less than subspecies rank' (Amadon & Short 1992). The implications of this study for the infraspecific taxonomy of other groups, in which even less is known about phenotypic plasticity of the bill (and perhaps other parts) than in the Great Tit, may be profound.

Summary

For over one-hundred years the Great Tit in Britain has been recognized as a distinct subspecies *Parus major newtoni*. All of the characters taken in the type to have been diagnostic have now been dismissed and modern diagnosis has been based, with scant evidence, on characters of the bill alone. Recent work has shown that the Great Tit bill is phenotypically plastic, varying seasonally in relation to changes in individual ecology. New data are presented here which support the earlier view that the British Great Tit is phenotypically distinct from *P. m. major*. Nevertheless, the validity of a taxon based on a single, phenotypically-plastic, trait is questioned in a modern context of evolution-based taxonomy. This may have implications for other taxa.

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Appendix

Type description of *Parus major newtoni* (Prazak 1894, p. 239). Translated from German by M. G. Wilson.

The British Great Tit differs from the continental bird on its smaller average size, and in having duller plumage although the colour pattern is the same. The black of the crown and the broad belly stripe are not as pure as in the continental bird and is almost without gloss. The cheeks are a dirtier white. The ash-grey of the rump is reduced to a minimum, being squeezed out by the olive-green of the back. The otherwise blueish ash-grey tail feather edges are—in the British bird—blackish, or at least much darker than in the central European specimens. The edges of the secondaries similarly show a marked suffusion with the back colour and the bar formed by the tips of the upper wing coverts is less clear and clean in colour. The yellow of the underside is less intense with a somewhat greenish flush.

L. Olph Galliard recognized this form as distinct from the European Great Tit but gave no name. I make so bold as to name this insular subspecies after the greatly honoured master of scientific ornithology at Cambridge, Professor A. Newton.

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